Latitudinal variation in life-history traits of bonnethead sharks, *Sphyrna tiburo,* (Carcharhiniformes:Sphyrnidae) from the eastern Gulf of Mexico

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Abstract. Life-history traits (size at age, growth rates, size and age at maturity, size of near-term embryos and litter sizes) of bonnetheads, *Sphyrna tiburo*, were analysed to test for latitudinal differences by comparing data collected from three areas along Florida's Gulf of Mexico coastline between March 1998 and September 2000. A total of 539 sharks were collected during the study: 207 in north-west Florida (latitude ∼30°N), 176 in Tampa Bay (∼28°N) and 156 in Florida Bay (∼25°N). Male and female bonnetheads in north-west Florida had the largest predicted asymptotic sizes (1007 mm and 1398 mm TL, respectively) and attained the largest estimated median size at maturity (830 mm and 944 mm, respectively) and the oldest estimated median age at maturity (3.0+ years and 4.0+ years, respectively). The largest near-term embryos (297 mm TL) were also collected at the highest latitude, but no latitudinal difference in litter size was found. These differences in life-history traits provide supporting evidence that a pattern of latitudinal variation exists. Male and female bonnetheads in north-west Florida also had the fastest growth rate compared with the other locations, supporting the hypothesis that growth rate is inversely related to the length of the growing season (i.e. a pattern of countergradient variation exists).

Extra keywords: growing season, growth rate, litter size.

Introduction

The environmental changes that occur with changing latitude have been shown to be important in altering, often in predictable ways, the life-history traits of various animal groups (Ray 1960; Sinero 1990; Inverson *et al.* 1993; Stergiou 1999). Biological characteristics directly affected by environmental conditions found at different latitudes include size-at-age, maximum size and age, size and age at maturity, growth rate and fecundity, to name a few. One of the more commonly observed trends is an increase in body size with an increase in latitude for species covering a large geographical area, which is commonly referred to as Bergmann's Rule (Mayr 1942).

Latitudinal variation in life-history traits has been demonstrated in various species of teleosts. For example, American shad, *Alosa sapidissima,* showed an increase in size-at-age from Florida, USA to New Brunswick, Canada (Leggett and Carscadden 1978). A latitudinal increase in

mean age at maturity was found in red bandfish, *Cepola macrophthalma*, and sea-run migrant brown trout, *Salma trutta* (L'Abée-Lund *et al.* 1989; Stergiou 1999). A positive relationship between growth rate and latitude was demonstrated for splitnose rockfish, *Sebastes diploproa* (Boehlert and Kappenman 1980), and coho salmon, *Oncorhynchus kisutch*, exhibited a positive relationship between egg number and latitude along the north-eastern Pacific Ocean (Fleming and Gross 1990). Similarly, growth rate, body size and sex determination were reported to have a positive relationship with latitude in Atlantic silversides, *Menidia menidia* (Conover and Present 1990; Lagomarsino and Conover 1993).

Although latitudinal variation has been extensively investigated in bony fishes, elasmobranchs have received less attention. At present, the effect of latitude on life-history traits of elasmobranch populations has been considered in only four published studies, three of them conducted in the
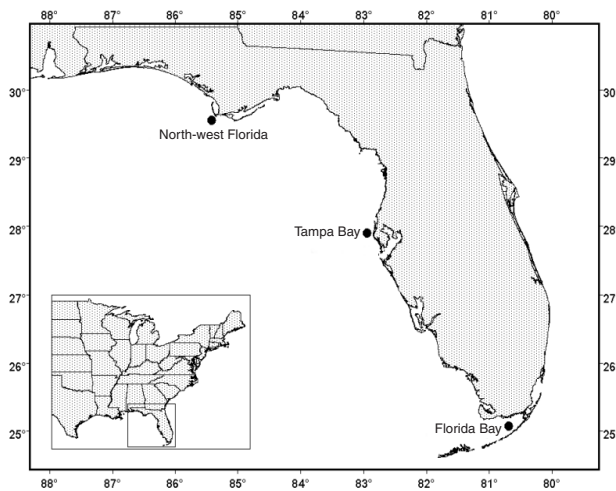
Fig. 1. The location of collection sites for bonnetheads sampled from 1998 to 2000.

North Pacific Ocean on starspotted dogfish, *Mustelus manazo* (Yamaguchi *et al.* 1998, 2000), cloudy catshark, *Scyliorhinus torazome* (Horie and Tanaka 2002) and shortnose spurdog, *Squalus mitsukurii* (Taniuchi *et al.* 1993). Lengths of adult female bonnetheads from three areas in the eastern Gulf of Mexico increased with latitude (Parsons 1993*a*, 1993*b*; Carlson and Parsons 1997), although no significant differences were found in the lengths of adult male bonnetheads or other traits, such as age at maturity of adult females. The failure of these studies to demonstrate a latitudinal trend in some life-history traits might have been due to low sample sizes and/or the fact that comparisons were made using data collected over 10 years (Cailliet *et al.* 1990; Parsons 1993*a*, 1993*b*; Carlson and Parsons 1997).

In the wake of these prior investigations, a study including contemporaneous sampling across sites and encompassing the entire eastern Gulf of Mexico was needed to more clearly describe the effect of latitude on bonnethead populations. To address this need, the present study examined the effect of latitude on bonnetheads, *Sphyrna tiburo,* from three geographical areas of the eastern Gulf of Mexico. Our objectives were to test for differences in size (i.e. mean adult size, maximum size), age and growth (i.e. growth, size-at-age, age at maturity, maximum age) and reproductive traits (i.e. near-term embryo weights and lengths, litter size) in relation to changes in latitude along the eastern Gulf of Mexico.

Materials and methods

Sharks were collected from three areas along the eastern Gulf of Mexico from March 1998 to September 2000: north-west Florida (~29°40′N, 85°13′W), Tampa Bay (~28°10′N, 82°42.5′W) and Florida Bay (~24°50′N, 80°48′W; Fig. 1). Sharks in north-west Florida were collected with gill-nets consisting of mesh sizes ranging from 8.8 to 14.0 cm in incremental steps of 1.3 cm (most sharks were collected in

nets with an 11.4-cm mesh size); sharks in Tampa Bay and Florida Bay were collected primarily in gill-nets with a mesh size of 11.4 cm. Before setting the gill-nets we recorded water temperature (°C), salinity, dissolved oxygen (mg L^{-1}) and a general description of the bottom composition (i.e. seagrass, mud or sand). When set, the nets were anchored at both ends. After capture, sharks were placed on ice and returned to the laboratory for further processing.

In the laboratory we recorded precaudal, fork, total and stretch total lengths (mm), weight (kg) and sex of the sharks. Maturity of male sharks was determined by the length and calcification of the claspers, whereas maturity in females was assigned using the diameter of the largest ovarian ovum, which is larger than 2 mm in mature bonnetheads (Parsons 1993*a*). Pregnancy was assessed in mature females and the size and sex of all embryos was recorded. For each shark, 5–10 vertebrae were removed from below the first dorsal fin. Vertebrae were separated, cleaned of excess tissue and placed in a 5% sodium hypochlorite solution for up to 15 min. After cleaning, vertebrae were stored in 95% isopropyl alcohol.

One vertebra was randomly selected from each shark. The vertebra was fixed to a slide with resin (complete embedding was not necessary) and sectioned using a Buehler Isomet low-speed saw. Numerous sectional thicknesses were tested and a thickness of 0.6 mm was chosen for sectioning and ageing all sizes of vertebrae because it resulted in the best readability of growth bands. The vertebral section was then mounted to a microscope slide with Cytoseal 60 mounting medium.

Age and growth

Growth bands were identified and counted on sections without staining. When viewed with transmitted light from a stereomicroscope, bands appeared as alternating broad opaque or narrow translucent regions in the corpus calcareum within the vertebral section. To estimate age from each vertebral section, we recorded the number of narrow translucent bands, corresponding to winter growth (November–February). Based on the validation results of Parsons (1993*b*), alternating pairs of bands (one opaque and one translucent) represent 1 year of growth. However, since the birthmark (translucent band) is deposited in late summer/early fall (July–September), only 6 months of growth are represented between the first and second translucent zones (Parsons 1993*b*). Therefore, a shark with one band (the birthmark) was assigned an age of 0+ years and a shark with two bands was assigned an age of 0.5+ years. Two readers recorded band counts for all specimens independently, without any meristic information.

Three indices of ageing error were calculated after each reader aged all sharks. The average percentage error (APE) between the readers' band counts was calculated following Beamish and Fournier (1981). The index of precision (D) was calculated by first determining the coefficient of variation (V) for each sample aged (Chang 1982). The percentage of readings in agreement was calculated as the total number of readings agreed on by both readers within ±1 and ±2 band counts, presented as a percentage of all readings (Chang 1982). Vertebral age estimates for which the readers disagreed were re-read by both readers using a Pixera digital camera and software (Pixera Studio V.2, Pixera Corporation). If no agreement was reached, samples were discarded from further analysis.

Determination of growth curves

Growth curves were constructed for females and males from each area separately using the von Bertalanffy (1938) theoretical growth model:

$$L_t = L_\infty \left(1 - e^{-K(t - t_0)}\right)$$

where L_t = length at age t, L_∞ = theoretical maximum length, t_0 = age at zero length, and K = growth coefficient. Parameters were estimated using least-squares non-linear regression (SAS version 8, SAS

Table 1. Life-history parameter estimates ± s.e. for male (M) and female (F) bonnetheads from north-west Florida (NWFL), Tampa Bay (TB) and Florida Bay (FB)

Size reported as total length (mm)

Parameters	NWFL	TB	FB
Sample size	92 (M)	84 (M)	69 (M)
	99 (F)	79 (F)	76 (F)
Theoretical maximum size (L_∞)	1007 ± 85 (M)*	868 ± 43 (M)*	858 ± 92 (M)*
	1398 ± 186 (F)*	1277 ± 203 (F)*	939 ± 58 (F)*
Growth coefficient (K)	0.35 ± 0.10 (M)*	0.44 ± 0.13 (M)*	0.25 ± 0.12 (M)*
	0.18 ± 0.05 (F)*	0.16 ± 0.07 (F)*	0.29 ± 0.09 (F)*
Theoretical age (years)	−0.31 ± 0.38 (M)*	−1.04 ± 0.64 (M)*	−2.66 ± 1.26 (M)*
at zero length (t_o)	−0.93 ± 0.44 (F)*	−2.39 ± 1.01 (F)*	−1.79 ± 0.82 (F)*
Median size at maturity	830 (M)	707 (M)	655 (M)
	944 (F)	823 (F)	770 (F)
Median age at maturity	3.0+ years (M)	1.6 years (M)	1.6+ years (M)
	4.0+ years (F)	2.9 years (F)	2.9+ years (F)
Observed maximum size	930 (M)	910 (M)	850 (M)
	1100 (F)	1040 (F)	1000 (F)
Observed maximum age	5.5+ years (M)	5.5 years (M)	5.5+ years (M)
	6.5+ years (F)	6.5 years (F)	7.5+ years (F)

*All pair-wise comparisons significantly different ($P < 0.001$), as determined from a likelihood-ratio test.

Institute, Inc., Cary, NC, USA). The parameters of the von Bertalanffy growth equation (L_∞, K, t_o) were compared using maximum likelihood ratio tests as proposed by Haddon (2001). This method, which assigns a degree of freedom for each parameter and does not assume equal variances, was used to determine differences between sexes within and between areas.

Growth rates were calculated from total lengths predicted by the von Bertalanffy growth model. Growth intervals were represented by the time between band deposition (e.g. growth interval one is the time between band counts one and two). Sex-specific predicted growth rates (cm year^{-1}) were compared among the areas.

Latitudinal differences in the size of adults were examined separately for males and females using single-factor, random-effects analysis of variance. On rejection of the null hypothesis ($P < 0.05$), a Tukey test for multiple comparisons was performed to detect differences between pairs of populations (e.g. between north-west Florida and Tampa Bay) (Zar 1999).

Maturity estimates for size and age

To determine maturity estimates, a logistic regression model was fitted to binomial maturity data (immature = 0, mature = 1) (Mollet *et al.* 2000). Separate models were fitted for males and females for each of the three areas. The median sex-specific size or age at maturity corresponds to the size or age at which 50% of the population reaches maturity. The model was fitted using the method of maximum likelihood (PROC LOGISTIC, SAS version 8, SAS Institute, Inc.). The effect of area was added to the logistic model to test for similarities in size and age at maturity between areas by sex (SAS version 8, SAS Institute, Inc.).

Reproductive effort

The relationships between maternal total length and lengths of near-term embryos, as well as the relationships between maternal total length and litter size were tested for each area. The lengths and weights of near-term embryos and the litter sizes were used as measures of reproductive effort. Near-term embryos were determined by the closeness of the date of capture of the pregnant female to the assigned date of birth for each area. The assigned date of birth for each area was based on reports of birth in Tampa Bay and Florida Bay (Parsons 1993*a*;

Tampa Bay: 15 August; Florida Bay: 15 July) and north-west Florida (Carlson unpublished data; 15 September). Latitudinal differences in litter size and in the lengths and weights of embryos were tested using a single-factor, random effects analysis of variance. On rejection of the null hypothesis ($P < 0.05$), a Tukey test for multiple comparisons was performed to detect differences between pairs of populations (e.g. between north-west Florida and Tampa Bay) (Zar 1999).

Results

Age and growth

We collected 539 vertebral samples during the study (207 in north-west Florida, 176 in Tampa Bay, and 156 in Florida Bay); 10% ($n = 40$) of these samples were discarded due to reader disagreement. The APE between readers was 8.6%, the index of precision was 0.09, and the percentage of readings in agreement within ±1 band count was 88.8%, increasing to 97.3% within ±2 band counts for the initial readings. Only those samples where both readers agreed on the number of bands were used in further analysis (i.e. in the determination of growth curves). The oldest shark aged was a mature female captured in Florida Bay with nine band counts, an age of 7.5+ years (Table 1). In general, females were older than males within each area. Significant differences in age were found between males and females in Tampa Bay and Florida Bay (Tampa Bay: *t*-statistic = 5.58, d.f. = 141, $P < 0.0001$; Florida Bay: *t*-statistic = 3.32, d.f. = 136, $P < 0.0001$); however, no significant difference in age between sexes was found in north-west Florida (*t*-statistic = 0.81, d.f. = 179, $P = 0.42$).

Females reached their theoretical maximum size (L_∞) at a slower rate (K) than males in north-west Florida ($K = 0.18$ and 0.35 year^{-1}, respectively) and Tampa Bay ($K = 0.16$ and 0.44 year^{-1}, respectively), but not in Florida Bay ($K = 0.29$ and
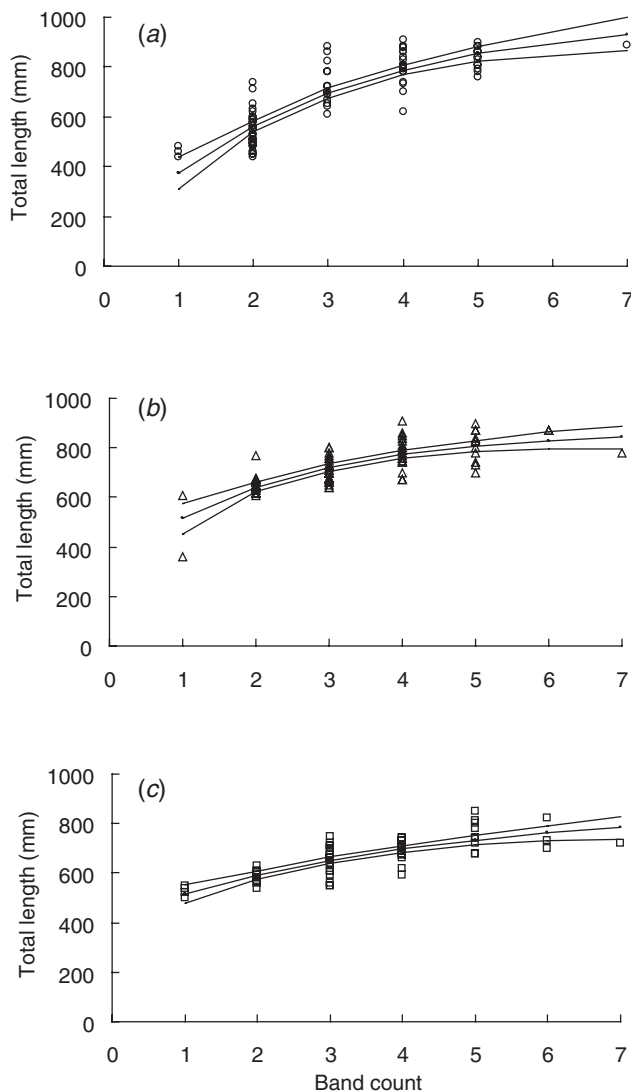
Fig. 2. Von Bertalanffy growth curves (±s.e.) fitted to observed size-at-age data for male bonnetheads collected from (*a*) north-west Florida, (*b*) Tampa Bay and (*c*) Florida Bay.
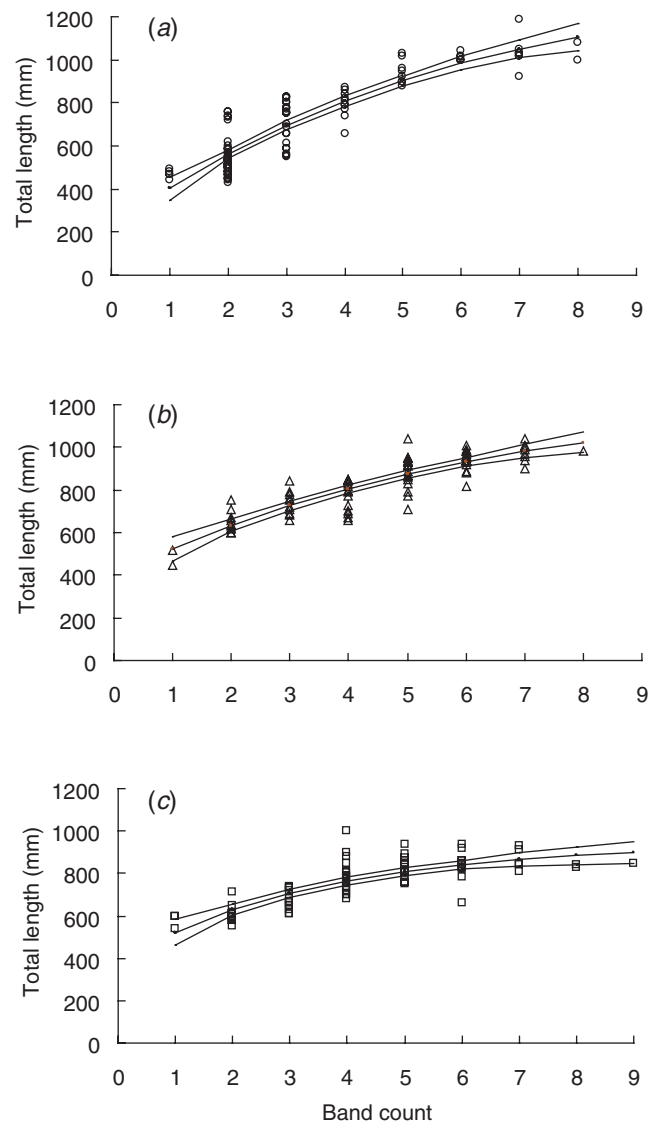

Fig. 3. Von Bertalanffy growth curves (±s.e.) fitted to observed size-at-age data for female bonnetheads collected from (*a*) north-west Florida, (*b*) Tampa Bay and (*c*) Florida Bay.

0.25 year^{-1}, respectively). The predicted asymptotic length (L_∞) was larger for females than males in each area. The largest predicted asymptotic lengths for males and females were for sharks from north-west Florida (1007 and 1398 mm TL, respectively; Figs 2, 3). Significant differences in the von Bertalanffy parameters were observed between sexes within each area (north-west Florida: likelihood ratio test (LRT) = 8.93, $P < 0.05$; Tampa Bay: LRT = 23.09, $P < 0.001$; Florida Bay: LRT = 35.81, $P < 0.001$). Significant differences in the von Bertalanffy growth parameters were also found for males and females between north-west Florida and Tampa Bay (males: LRT = 30.70, $P < 0.001$; females: LRT = 19.76, $P < 0.001$), Tampa Bay and Florida Bay (males: LRT = 55.11, $P < 0.001$; females: LRT = 39.52, $P < 0.001$), and north-west

Florida and Florida Bay (males: LRT = 56.84, $P < 0.001$; females: LRT = 58.61, $P < 0.001$).

Based on predicted sizes, males and females from north-west Florida had faster growth rates (cm year^{-1}) at each growth interval than their counterparts from Tampa Bay and Florida Bay (Fig. 4). Female bonnetheads from Florida Bay had the slowest growth rate among areas at all growth intervals. Tampa Bay males had growth rates similar to those of Florida Bay males beginning with band count three (1.5+ years).

Significant differences in observed lengths were found for adult male and adult female bonnetheads between the three areas (males: $F = 49.95$, $P < 0.0001$, d.f. = 2; females: $F = 55.97$, $P < 0.0001$, d.f. = 2; Fig. 5). Tukey *post hoc* tests
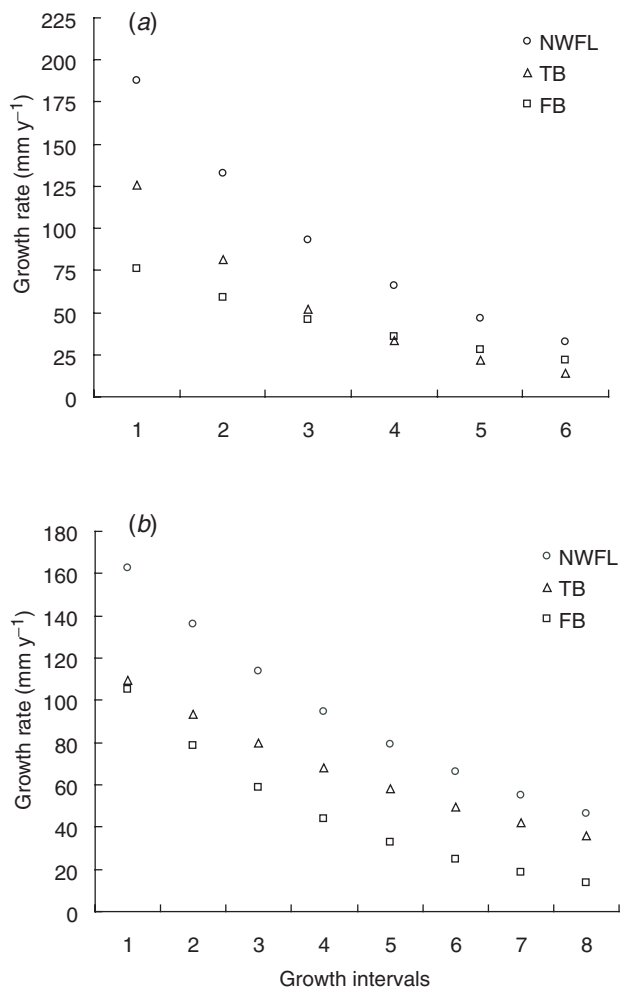
Fig. 4. Growth rates from predicted sizes at age for (*a*) male and (*b*) female bonnetheads from north-west Florida (NWFL), Tampa Bay (TB) and Florida Bay (FB). Growth interval is the time between band depositions (i.e. growth interval one equals 6 months, growth intervals ≥2 equal 1 year).

Fig. 5. Length–frequency histograms of (*a*) adult male and (*b*) adult female bonnetheads from north-west Florida (NWFL), Tampa Bay (TB) and Florida Bay (FB). Sample sizes are reported in legends.

further detected significant differences in length of adult males and females between all pairwise comparisons ($P < 0.05$). North-west Florida adult males and females attained the largest average size (851 ± 37 s.d. and 1016 ± 57 s.d. mm TL, respectively). Florida Bay adult male and female bonnetheads had the smallest observed mean size (713 ± 50 and 850 ± 53 mm TL, respectively (mean $\pm$ s.d.)). Adult males and females in Tampa Bay reached an intermediate mean size compared with the other two areas (786 ± 61 and 930 ± 57 mm TL, respectively (mean $\pm$ s.d.)).

Maturity estimates for size and age

The largest median size and age at maturity for males and females were those from north-west Florida (males: 830 mm, 3.0+ years of age; females: 944 mm TL, 4.0+ years of age; Figs 6, 7). Significant differences in size at maturity estimates
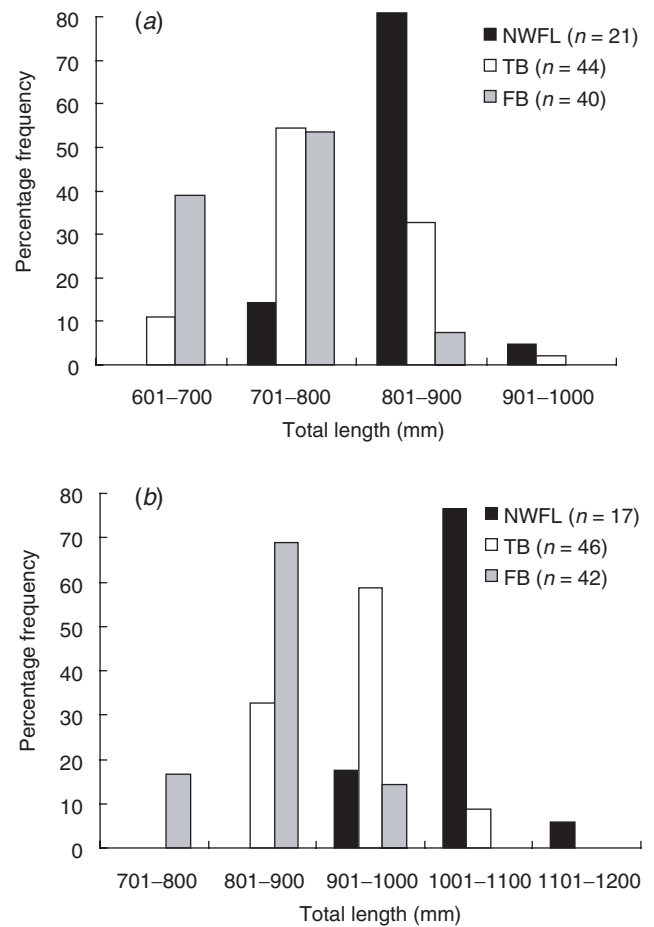
were found for males and females between north-west Florida and Tampa Bay (males: effect of area maximum likelihood estimate $= -2.42$, $P < 0.0001$; females: -2.82, $P = 0.0002$), Tampa Bay and Florida Bay (males: 1.31, $P < 0.0001$; females: 2.26, $P = 0.0030$), and north-west Florida and Florida Bay (males: 3.31, $P < 0.0001$; females: 3.96, $P < 0.0001$). Significant differences in age at maturity estimates were also found for males and females between north-west Florida and Tampa Bay (males: -1.16, $P < 0.0001$; females: -0.98, $P = 0.0022$) and north-west Florida and Florida Bay (males: 1.16, $P < 0.0001$; females: 0.99, $P = 0.0018$). No significant differences in age at maturity were detected for males or females between Tampa Bay and Florida Bay (males: -0.005, $P = 0.98$; females: 0.01, $P = 0.73$). The median age at maturity was the same in Tampa Bay and Florida Bay for males and females, 1.6+ years of age and 2.9+ years of age, respectively (Fig. 6, 7).

Reproductive effort

A significant linear relationship between maternal total length and near-term embryo total length was found for
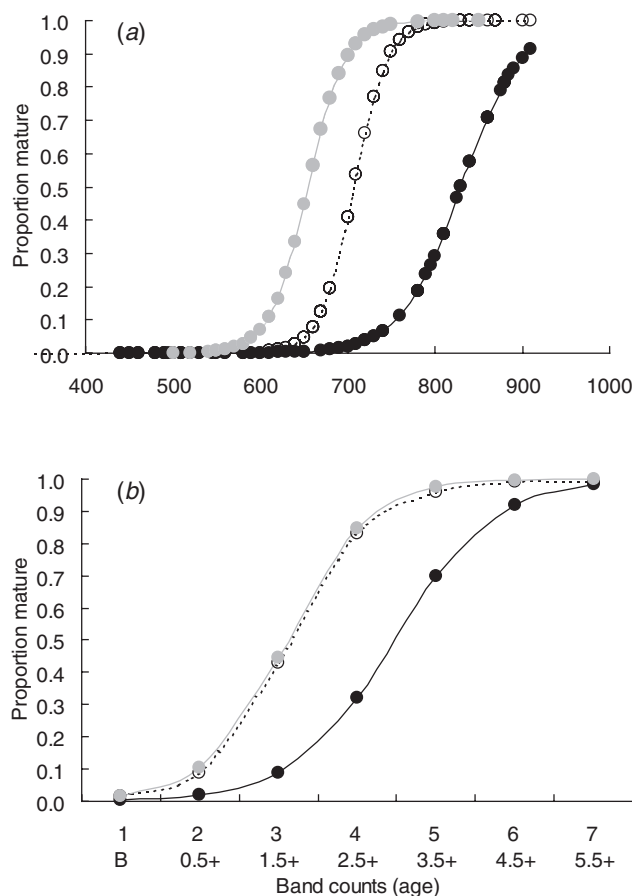
Fig. 6. Maturity estimates for male bonnetheads (*a*) total length and (*b*) age for north-west Florida (●), Tampa Bay ○, dotted line) and Florida Bay (⬤).
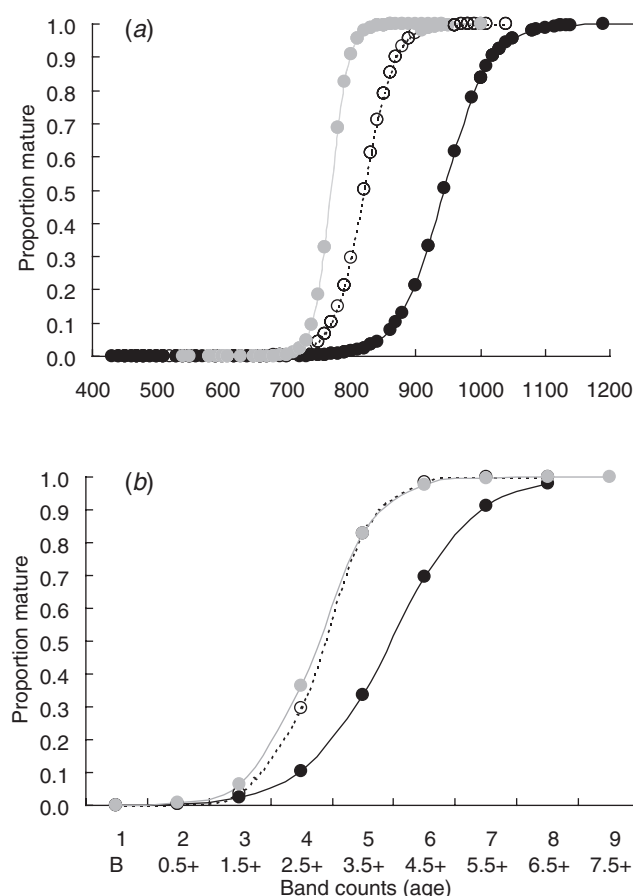

Fig. 7. Maturity estimates for female bonnetheads (*a*) total length and (*b*) age for north-west Florida (●), Tampa Bay ○, dotted line) and Florida Bay (⬤).

north-west Florida and Florida Bay (north-west Florida: $r^2 = 0.35$, $P < 0.0001$, $n = 30$; Florida Bay: $r^2 = 0.64$, $P < 0.001$, $n = 15$), but not for Tampa Bay ($r^2 = 0.02$, $P = 0.43$, $n = 37$). In addition, the only significant linear relationship between maternal total length and litter size was found for Tampa Bay ($r^2 = 0.27$, $P = 0.02$, $n = 19$), with both north-west Florida and Florida Bay having non-significant linear relationships (north-west Florida: $r^2 = 0.04$, $P = 0.48$, $n = 14$; Florida Bay: $r^2 = 0.03$, $P = 0.53$, $n = 17$). Significant differences in the lengths and weights of near-term embryos were detected among the three areas (length: $F = 177.17$, $P < 0.0001$, d.f. = 2; weight: $F = 148.63$, $P < 0.0001$,

d.f. = 2). The largest near-term embryos occurred in north-west Florida, with a mean length of 297 mm (TL) and weight of 97 g, and the smallest embryos occurred in Florida Bay, with a mean length of 215 mm (TL) and weight of 35 g (Table 2). Tukey *post hoc* tests further revealed significant differences in near-term embryo lengths and weights for all pairwise comparisons ($P < 0.05$). No significant differences were detected for litter sizes among the three areas (Table 2).

Discussion

As discussed by Cailliet *et al.* (1990) and Tanaka *et al.* (1990), detecting real differences in growth estimates might

Table 2.   Reproductive parameters (mean ± s.d.) for bonnetheads from north-west Florida (NWFL), Tampa Bay (TB) and Florida Bay (FB)

Sample sizes in parentheses *(n)*

Parameters	NWFL	TB	FB
Near-term embryo total length (mm)	297 ± 22 (30)*	237 ± 7 (38)*	215 ± 18 (15)*
Near-term embryo weight (g)	97 ± 21 (30)*	44 ± 6 (38)*	35 ± 10 (15)*
Litter size	11 ± 3 (14)[NS]	10 ± 3 (19)[NS]	10 ± 3 (17)[NS]

*All pair-wise comparisons significantly different ($P < 0.05$), as determined from *post hoc* Tukey tests.
[NS], Non-significant.

be difficult. Differences in vertebral preparation, sample sizes, and inter-reader variability in band counts could produce variations in growth rates that are not real. We minimised most sources of bias by using the same technique for vertebral sectioning and ageing, had two readers with 100% agreement in band counts, sampled all areas during the same period, and had samples from all sizes of sharks at comparable numbers from all areas.

Our results provide a more complete picture of the effects of latitudinal variation on bonnethead life-history traits compared to previous studies of this species. Although significant differences in sizes of adult female bonnetheads have been demonstrated for some eastern Gulf of Mexico areas (Parsons 1993*a*, 1993*b*; Carlson and Parsons 1997), no study had demonstrated latitudinal variation in adult body size for both sexes across the entire eastern Gulf of Mexico. In addition, our estimates of size and age at maturity and size (length and weight) of near-term embryos also increased with latitude. The trends we detected are probably due to a larger sample size for adult males in both Tampa Bay (Carlson and Parsons 1997, *n* = 26; present study, *n* = 46) and Florida Bay (Carlson and Parsons 1997, *n* = 11; present study, *n* = 41). Furthermore, the fact that our samples were collected simultaneously in all three areas precludes the possibility that the observed differences were the result of interannual variation in life-history traits.

Although Bergmann's rule (Mayr 1942) is generally thought to apply to homeotherms, evidence suggests that it might also apply to aquatic marine poikilotherms (Conover 1990). Statistically significant different sex-specific mean adult size and estimated median size and age at maturity for both males and females were detected for bonnetheads from the three areas, with the largest and oldest bonnetheads found in more northern areas. Similarly, trends of increasing size at maturity with latitude were reported for both sexes of cloudy catshark, *Scyliorhinus torazame* (Horie and Tanaka 2002), shortspine spurdog, *Squalus mitsukurii* (Taniuchi *et al*. 1993), and female starspotted dogfish, *Mustelus manazo* (Yamaguchi *et al*. 2000), but none of these studies reported any statistically significant differences in sex-specific size at maturity between their corresponding areas of study. Latitudinal differences are thought to be an adaptive response of an individual to different environmental factors, but the mechanisms underlying it are controversial and might be controlled by physiological constraints or genetic factors (Levins 1969; Conover 1990). Preliminary evidence from mitochondrial DNA suggests that there are no sharp genetic discontinuities between bonnethead populations from these areas (Demian Chapman, Nova University/Guy Harvey Research Institute, personal communication), which lends support to the hypothesis that differences detected in life-history traits of bonnetheads are caused by a phenotypic response to differences in environmental factors.

The lengths and weights of near-term embryos were also consistent with the predictions of latitudinal variation, with the largest embryos found at the highest latitudes. Parsons (1993*a*) also detected this latitudinal increase in offspring size for bonnetheads between Florida Bay and Tampa Bay. This trend was not examined in the viviparous shortspine spurdog (Taniuchi *et al*. 1993) and results were inconclusive in the starspotted dogfish (Yamaguchi *et al*. 2000); in oviparous catsharks no trend was found in egg capsule size with latitude in the north Pacific (Horie and Tanaka 2002). Thus, more research is needed to establish how reproductive mode (viviparous *v.* oviparous) influences latitudinal variation in life-history traits of elasmobranchs (Cortés 2000).

Despite the fact that mature females in Tampa Bay and north-west Florida are larger and potentially capable of producing larger litter sizes than those in Florida Bay, no difference in mean litter size was found among the three areas. Likewise, Parsons (1993*a*) detected no difference in bonnethead litter sizes from Tampa Bay and Florida Bay. Life-history theory would predict that female bonnetheads optimise offspring production either by increasing or decreasing the number of offspring and producing an appropriately sized offspring to maximise survivorship (Smith and Fretwell 1974). Because no relationship between maternal size and the number of offspring was found in north-west Florida, it appears that females produce larger offspring at higher latitudes to increase survivorship, thereby potentially reducing over-winter mortality. Water temperatures during the winter months (November– February) were significantly different between areas, with north-west Florida being the coldest (15.7 ± 3°C; NOAA/NOS/Center for Operational Oceanographic Products and Services satellite monitoring stations). Furthermore, bonnetheads in north-west Florida give birth later than their counterparts in Florida Bay (September *v.* July), but the gestation periods are the same. Sharks or teleosts born closer to the end of the first summer growing season would need to be larger to survive their first winter (Conover and Present 1990).

Growth rates at higher latitudes were faster, perhaps because of the inverse relationship between growing season and latitude, also known as countergradient variation (Conover and Present 1990). Male and female sharks in north-west Florida (highest latitude) had the fastest growth rate at each growth interval. Sharks in Florida Bay (lowest latitude) exhibited the slowest and somewhat more uniform growth rates throughout their life, which could be due to the consistency of environmental conditions throughout the year. Faster growth rates might be a mechanism for the individuals at the highest latitude to compensate for the shorter growth season by growing faster during a shorter time period.

In this study, contemporaneous sampling over the entire eastern Gulf of Mexico produced results that further support latitudinal variation in life-history traits of bonnetheads as

first observed by Parsons (1993*a*, 1993*b*). Although there is only a latitudinal separation of five degrees among the sample sites, sharks from these areas displayed statistically different life-history traits. In summary, latitudinal variation was detected in sex-specific adult body size, estimated median length and age at maturity, and lengths and weights of embryos. In addition, the increase in growth rates with an increase in latitude provides evidence for countergradient variation (Conover and Present 1990) in this species, a phenomenon never before documented in elasmobranchs.

Acknowledgments

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